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Modelling the population dynamics of *Isotoma notabilis* (Collembola) on sites of different agricultural usage

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Summary. A model for the simulation of the population dynamics of Collembola under field conditions is presented. After calibrating the model on pasture land it was validated on five different agricultural sites grown with sugar beets, cereals and beans. On four of the six sites the simulation period was two years, on the remaining two sites three years. A good agreement between field measurements and simulation results was obtained. Because the simulation period included the winter time it was shown that the model is applicable to a broad range of climate conditions. This simulation model can be used to analyze the environmental impact (e.g. pesticides, tillage) on the population dynamics of Collembola.

Key words: Collembola, *Isotoma notabilis*, Leslie model, population dynamics, simulation models

Introduction

Only rudimentary Collembola populations of the original woodlands survive on agricultural land. So far little is known about the population dynamics of these Collembola communities. Because of the difficulty of interpreting the time courses, only a few investigations of the population dynamics under field conditions can be found in the international literature. Special studies on e.g. growth, fertility and mortality have been carried out in different laboratories (e.g. Choudhuri 1963; Davidson 1934; Longstaff 1977; Sharma & Kevan 1963; Snider 1974). Such investigations are necessary to understand the population dynamics observed in the field. Further complication in analyzing measurements arise because of the spatial and temporal heterogeneity in field conditions.

Nowadays, more studies concentrate on the role of the mesofauna for the transformation process of litter, but to quantify the transformation capacity of a specific population of soil animals the dynamics of these species has to be known. Another point of interest is the impact of environmental pollution on the population dynamics of the soil fauna. In order to evaluate those influences it is necessary to study the population dynamics under natural conditions.

Field measurements are time consuming and expensive. Therefore, it will be helpful to have a predictive tool to forecast the population dynamics of single species. The aim of this study is to present a dynamic model for *Isotoma notabilis* (Schäffer). This species was found permanently in a sufficient amount on six different sites investigated during the years 1986–1988.

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Different kinds of model approaches are available. The simplest approach is a regression model in which the results depend in a linear or a non-linear way on one or more variables. The application of such a static model on forecasting the population dynamics fails because the predicted population size on a certain date only depends on the input variables and not on the actual population size and structure. Although the parameters of a regression model are easy to obtain this model approach suffers from some weakness: The model has no explanatory power because the model structure is determined by the data available for model development and not on biological knowledge. In contrast to static models the dynamic model approach describes the population dynamics at time $t + \Delta t$ depending on environmental factors and the population size at time t.
The parameters of dynamics models often have a biological, physical or chemical meaning. In this case they can be derived from independent measurements like laboratory experiments. Parameters which can not be determined independently are usually calibrated by obtaining the best comparison between measured and observed values by varying model parameters. Calibration can be carried out manually or automatically in which case it is called parameter estimation. Because a model is developed according to actual knowledge calibration is often successful but this is no guarantee that the model works in other situations. In order to evaluate the applicability of the model the calibrated model has to be validated using measurements not used for calibration purposes. Validation entails confirming whether a model is able to simulate the observed population dynamics on other sites or for another period of time without modifying any model parameter. Before a model can be used as a predictive tool it has to be validated.
The parameters influence the model results at different orders of magnitude. A sensitivity analysis measures "how important" a parameter is for the predicted population dynamics. This analysis is carried out by varying each parameter separately and evaluating the results by comparing e.g. the temporal pattern, the maximum abundances or the number of generations per year. From such an analysis it may be concluded which paramters do not have strong influence on the results. Then, it is not necessary to spend too much effort to determine these parameters.
A detailed description of all aspects concerning modelling of agro-ecosystems is given by Rohdenburg (1989) and concerning modelling of population dynamics by Caswell (1989).

Materials and Methods

Simulation model

Models for the simulation of population dynamics have been developed for a long time. When applying these models to insect populations the different stages (phases) which can be observed in the life cycle of these insects have to be considered. In the case of Collembola (according to Longstaff (1977) and other authors) four different stages have to be distinguished: egg, juvenile, reproductive, post-reproductive.
One of the classical approaches for modelling the population dynamics while incorporating an age structure is that of Leslie (1945, 1948). This matrix model is frequently used. For example Longstaff (1977) applied this model to simulate the population dynamics of *Onychiurus armatus* and *Hypogastrura denticulata* (Collembola). He considered five different classes: Class 1 and 2 represented the juvenile phase, class 3 and 4 the reproductive phase and class 5 the post reproductive. He applied his model to laboratory measurements and found a good agreement with the simulation results. The disadvantage of his model is that the population dynamics is described for constant temperatures which are valid only under laboratory conditions.
This model approach is not applicable under varying temperature regimes because different development rates for each of the stages have to be considered. The classical Leslie approach was further developed by Söndgerath & Richter (1990). They assumed a Leslie process for each stage. Then, the total model is a combination of a number of Leslie processes. A schematic representation of this approach as used in this study can be found in Fig. 1. A detailed description of the mathematical preliminaries is given by Söndgerath & Richter (1990). Therefore, in this study only the basic ideas of the model are presented.

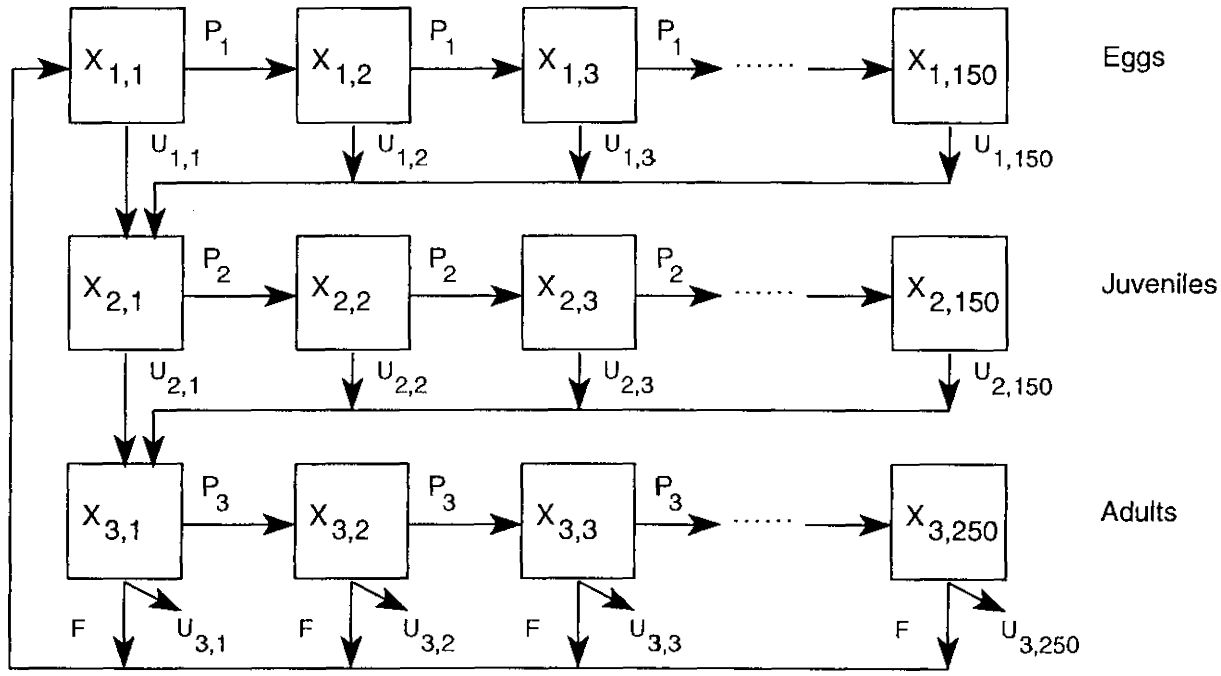

Fig. 1. Structure of the Leslie-model as used in this study: $x_{s,i}$ = number of individuals in stage s class i, P_s = survival probability of stage s, $U_{s,i}$ = transition probability of stage s class i, F = fertility [eggs/day]

Each development stage is divided into a number of classes (cf. Fig. 1). For each class the number of individuals is calculated. The individuals in each class have the chronological age of the class number times the time step Δt. An appropriate number of classes has to be chosen in order to ensure that only a few individuals reach the last class. The model is calculated in discrete time steps. Due to the expected development rates a time step of 24 hours was chosen in this application.

For the description of the development of insects under varying environmental conditions the chronological age is inadequate (Van Sickle 1977). He and others found that the temperature has the greatest impact on the development rate. Therefore, it is important to distinguish between chronological age and state of development. In this model the time measure is the chronological age but the measure of development is a transformation of this age considering the temperature. This transformation is called biological age t_{biol} and can be calculated as the integral over the development rate r which on their part depends on the temperature (Söndgerath & Richter 1990).

$$t_{\text{biol}} = \int_0^t r(T(t^*))\,\mathrm{d}t^* . \tag{1}$$

in which r = rate of development [1/days], T = temperature.

In order to obtain a normalized development time which is comparable for all conditions, the biological age of each stage was scaled to one. This means that the development rate of each stage under constant temperature was calculated as $1/n$ in which n equals the days required for development of this stage. In this case the development is finished when the biological time reaches one. The approach describing the temperature dependent development rate $r(T)$ will be discussed later (cf. model parameters).

The stages (egg, juvenile, adult) are linked via transition probabilities U_{si} (cf. Fig. 1). According to Söndgerath & Richter (1990) $U_{si}(t)$ is the probability that an individual in age class i of stage s at time t will develop into an individual of age class 1 of stage $s + 1$, e.g. that an egg will hatch. If the natural variability from individual to individual within a population is neglected then the development of all individuals within each stage is finished simultaneously when the biological time equals one. Considering the natural variability it is necessary to choose a distribution function G which describes the deviation from the mean development time. Söndgerath & Richter (1990) found the distribution function G to be of a Weibull distribution type. The transition probability U_{si} at time t can then be calculated from this distribution function:

$$U_{si} = \frac{G(t_{\text{biol}}(t)) - G(t_{\text{biol}}(t-1))}{1 - G(t_{\text{biol}}(t-1))}, \tag{2}$$

$$G = 1 - \exp\left(-(t_{\text{biol}})^{\beta}\right) \tag{3}$$

with β = slope of the Weibull distribution.

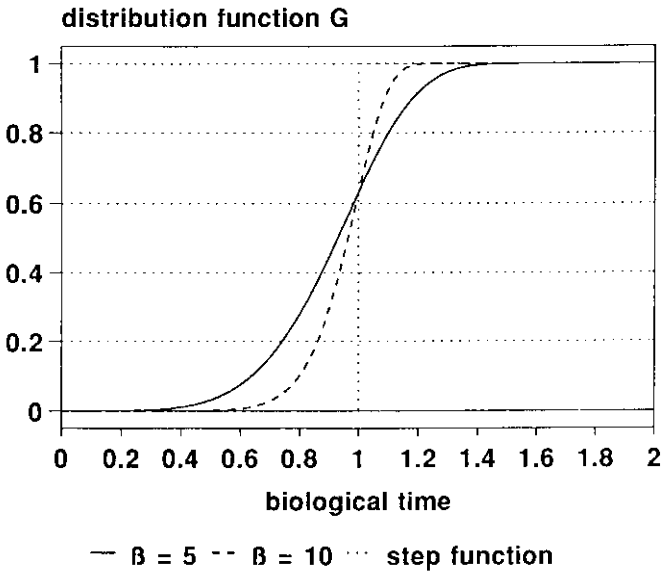

Fig. 2. Cumulated transition probability described by the Weibull function (cf. Eqn. 3) for two different values for β. This function is used to describe the natural variability of development within a population. When this natural variability is neglected a step function describes the transition from one stage to the next

A detailed description of the mathematical assumption necessary to obtain Eqns. 2 and 3 are given by Söndgerath & Richter (1990) and will not be discussed here. Fig. 2 shows the Weibull distribution function for two different values of β. In this study no data were available to estimate this parameter. From the data of Sharma & Kevan (1963) it can only be concluded that the variability from individual to individual is low. For example the authors reported that at 8 °C the mean time required for hatching varies between 30 and 32 days with a mean of 30.5 days. A low variability can be described by large values for β. Due to the observations of Sharma & Kevan, and sensitivity analyses carried out, β was fixed at the value of ten (Röske 1993).

In this simulation three different stages were considered: Eggs (1), juveniles (2) and adults (3) (cf. Fig. 1). Due to lack of data the adults were not differentiated into reproductive and post-reproductive individuals which is opposite to the approach of Longstaff (1977). Because the post-reproductive phase does not contribute to the increase of the population size and only few adults were caught (Röske 1993) this simplification is considered to be acceptable. For each timestep Δt a set of equations as described below has to be solved (Söndgerath & Richter 1990).

The number of individuals of a class $i + 1$ are calculated from the number of individuals of class i multiplied by the survival probability P_s. From this amount the number of individuals which finished the development of this stage in this timestep ($U_{s,i}$) are substracted:

$$x_{s,i+1}(t+1) = (1 - U_{s,i}(t))\, P_s x_{s,i}(t) \qquad s = 1 \ldots 3 \qquad i = 1 \ldots ns - 1\,. \tag{4}$$

For the last class ns of each stage s the number of individuals of class ns having survived from the last time step have to be added:

$$x_{s,ns}(t+1) = 1 - U_{s,ns-1}(t))\, P_s x_{s,ns\ \ 1}(t) + (1 - U_{s,ns}(t))\, P_s x_{s,ns}(t) \qquad s = 1 \ldots 3\,. \tag{5}$$

The number of individuals for class 1 at stage 2 (juveniles) and 3 (adults) are calculated as the sum of the individuals which hatched or finished the juvenile stage in this timestep:

$$x_{s,1}(t+1) = \sum_{i=1}^{n(s-1)} (U_{s-1,i}(t)\, x_{s-1,i}(t)) \qquad s = 2, 3\,. \tag{6}$$

The number of eggs laid (class 1 of stage 1) is computed by the number of adults multiplied by the fertility rate F:

$$x_{1,1}(t+1) = \sum_{i=1}^{n3} (F(T(t))\, x_{3,i}(t))\,. \tag{7}$$

where $x_{s,i}$ = number of individuals in stage s class i [ind./m^2], ns = number of classes of stage s (here $n1 = n2 = 150$, $n3 = 250$), P_s = survival probability of stage s, $U_{s,i}$ = transition probability of stage s class i, F = fertility [eggs/day], T = temperature [°C], t = time [days].

A detailed description of this model is presented by Söndgerath & Richter (1990). A first application to field data is given by Söndgerath & Müller-Pietralla (1994). In that paper the authors simulated the population dynamics of *Delia radicum* L. (Diptera: Anthomyiidae) and found a good comparison with field measurements.

Depending on the chosen parameters the predicted population will collapse or grow geometrically. Both cases are unrealistic. In contrast to this behavior a maximum population size depending on environmental conditions is often observed. According to Leslie (1948) this can be considered in two different ways: a) the fertility is constant and the survival probabilities (P_s) depend on the population size; b) the survival probabilities are constant and the fertility F depends on the population size. Longstaff (1977) observed a decrease in fertility with an increase of the population size for the Collembola *O. armatus* and *H. denticulata*. This behavior can be described by multiplying the fertility rate by a function $\varphi(k)$ which depends on the population size. According to Caswell (1989) density dependent models can show unstable solutions under constant environmental conditions. This phenomenon is not important for this study because the population size approaches the maximum on only a few occasions per year. In that case the density function has no lasting effect on the model results. To consider the density effect the following function $\varphi(k)$ (Richter et al. 1991), which describes the behavior as found by Longstaff (1977), was incorporated into the extended Leslie model:

$$\varphi(k) = \begin{cases} 1 - \left(\dfrac{k}{k_{\max}}\right)^{v} & \text{for} \quad k < k_{\max} \\ 0 & \text{for} \quad k \geq k_{\max} \end{cases}, \tag{8}$$

with k = population size (number of juveniles + adults) [ind./m^2], $k_{\max}$ = max. population size [ind./m^2], v = slope (constant value of 6 for all simulations).
Only qualitative information on parameter v could be obtained from the study of Longstaff (1977). Following a sensitivity analysis in which it was shown that this parameter was not very sensitive it was set to a constant value of 6.

Model parameters

The data needed to describe the development of *I. notabilis* under different temperatures were taken from a paper given by Sharma & Kevan (1963). They investigated *I. notabilis* under laboratory conditions using temperatures in the range of 4° to 17 °C. Although it has been known for a long time that a linear relationship between development and temperature (day-degree method) is appropriate only for a small range of temperatures, this method is often applied in simulation models (Logan & Hilbert 1983). The data of Sharma & Kevan (1963) show a nonlinear correlation between development rate and temperature. Furthermore, a decrease of the development above an optimal temperature which is often observed cannot be handled with the linear approach. In order to consider these phenomena the nonlinear function of O'Neill (Spain 1982) was chosen to be fitted to the data:

$$r(T) = \begin{cases} r_{\max}\left(\dfrac{T_{\max} - T}{T_{\max} - T_{\text{opt}}}\right)^{x} e^{x(T - T_{\text{opt}})/(T_{\max} - T_{\text{opt}})} & \text{for} \quad T \leq T_{\max} \\ 0 & \text{for} \quad T > T_{\max} \quad \text{and} \quad T < 0 \end{cases}, \tag{9}$$

in which

$$x = \frac{1}{400}\left[(q-1)(T_{\max} - T_{\text{opt}})\left(1 + \sqrt{1 + \frac{40}{(q-1)(T_{\max} - T_{\text{opt}})}}\right)\right]^2, \tag{10}$$

where $r(T)$ = development rate [1/days], T = mean daily temperature [°C], T_{opt} = optimal temperature [°C], $T_{\max}$ = maximal temperature [°C], $r_{\max}$ = maximal development rate at the optimal temperature [1/days], q = slope.
Fig. 3 shows the development rate of the eggs, Fig. 4 the rate of juvenile individuals. As can be seen in Fig. 3 and 4 no information about the optimal and the maximal temperatures can be gathered from the data. According to a paper given by Thibaud (1977) the optimal temperatures for *I. notabilis* were estimated to be 18° – 22 °C. Because only a few days with mean soil temperatures above 17 °C occurred during the investigated period (see Fig. 6a) this parameter is expected to be not sensitive. No information is given about the life time of adults, but Sharma & Kevan studied the number of ovipositions in the life cycle of *I. notabilis*. From these information the length of the productive phase of the adults can be estimated.

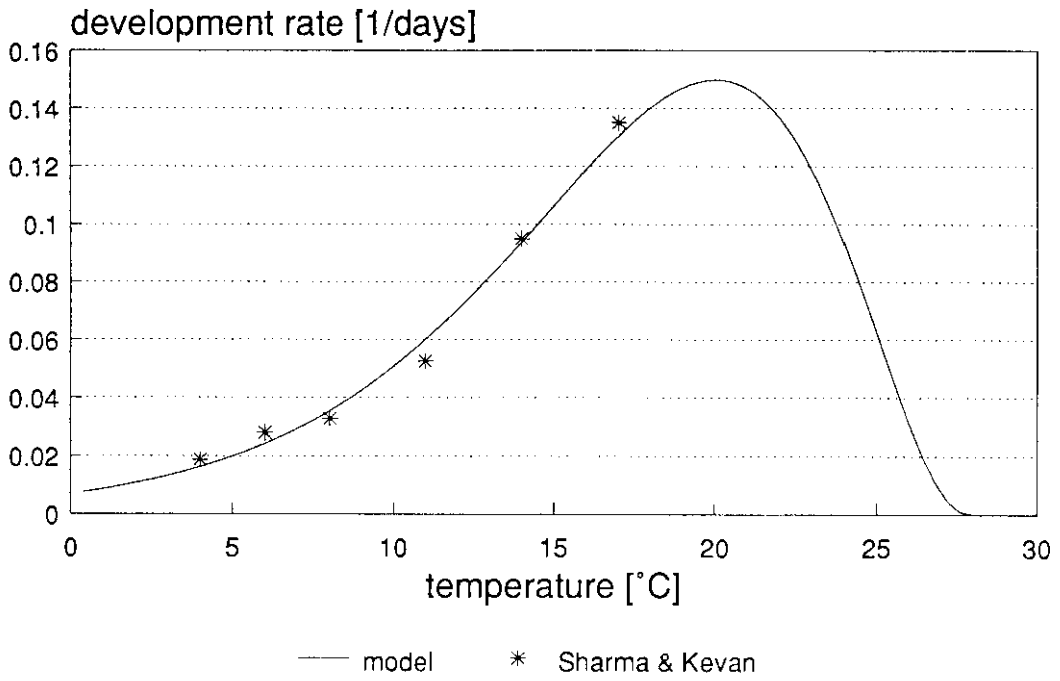

Fig. 3. Temperature dependent development rate for eggs. The data are taken from Sharma & Kevan (1963)

Within the paper of Sharma & Kevan (1963) the survival probability is given only for eggs under three different temperatures. No information about the survival probabilities of juveniles and adults can be found. Therefore, these parameters were calibrated during the simulation for the pasture land (see model application).

According to the data of Sharma & Kevan (1963) the number of ovipositions and the number of eggs laid per oviposition are temperature dependent. Because not enough information about the correlation between the number of ovipositions and the age of the individuals were available for *I. notabilis*, it was decided to describe the fertility only in terms of dependence on the temperature. Although the data do not show an optimal and a maximal temperature it was decided to use the approach of O'Neill (cf. Eqn. 9 and 10) to describe the number of eggs laid (Fig. 5). In order to obtain a good agreement with the observations a constant value had to be added to the O'Neill-function. This constant accounts for the fact that Sharma & Kevan (1963) observed that at 0 °C no eggs were laid. This can only be described by a constant added to the original O'Neill-function. The same good fit can be obtained using a polynom regression. But when this regression function is applied to temperature above 17 °C an unrealistically high fertility will be calculated (cf. Fig. 5). If further investigations show the necessity to consider the dependency of the number of ovipositions on age it poses no problem to modify the simulation model as Söndgerath & Müller-Pietralla (1994) showed in their study.

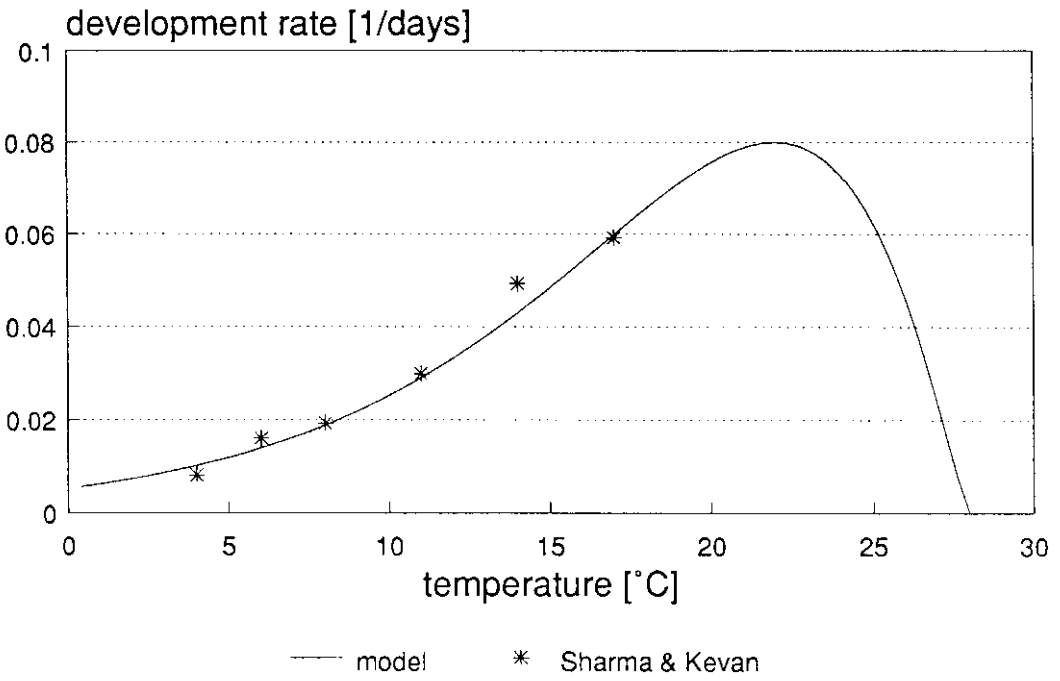

Fig. 4. Temperature dependent development rate for juveniles. The data are taken from Sharma & Kevan (1963)

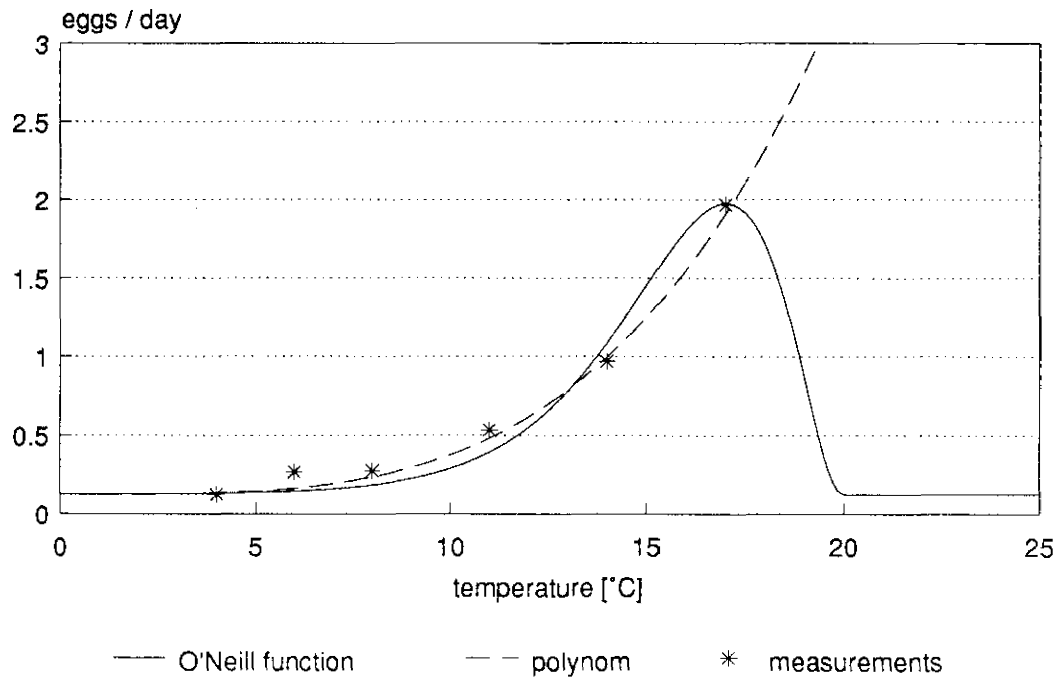

Fig. 5. Temperature dependent fertility rate. The data are taken from Sharma & Kevan (1963)

Sharma & Kevan (1963) found no parthenogenesis during their investigations. Petersen (1971) showed that parthenogenesis may occur in *I. notabilis*. During the year 1986 the individuals caught on site B were examined for their sex. In that year no males were found. First model tests with the fertility data of Sharma & Kevan lead to an overestimation of the population size. In a limited temperature range this can be compensated by reducing the survival probability but under these conditions the population size will collapse during the winter season. Petersen (1971) found a significant lower fertility than the one observed by Sharma & Kevan although he found parthenogenesis. Therefore, for this study the dependency of the fertility on the temperature was taken from Sharma & Kevan while the fertility rate at the optimal temperature was calibrated. The calibrated fertility rate is about 25% of the fertility rate observed by Sharma & Kevan. This is nearly the same value Petersen found in his investigations.
Because of the large variability of the field data and the unknown number of eggs in the soil it is not possible to use measurements for calculating the initial population size for the simulation. In particular the age structure of the population at the beginning of the simulation is unknown. To overcome this problem the model was started with a given number of individuals in stage 1 (eggs) class 1. The model was run for several years. After this long simulation period a typical age structure for the winter time was established. This typical age distribution was taken as the initial condition for all further simulations.

Field measurements

The field measurements were carried out during the years 1986–1988 in two different catchments. One catchment is situated about 70 km north of Braunschweig, Germany, where mainly sandy soils occur. The other catchment lies about 35 km south of Braunschweig. Silty, clayey and stony quaternary sediments dominate this catchment. The mean annual temperature of both catchments is about 9 °C, the mean annual rainfall lies between 650 (south) and 700 mm (north). In addition to the natural rainfall the northern catchment is irrigated with about 125 mm/year. In each catchment three different sites were investigated. A summarized description of the sites can be found in Tab. 1.

Table 1. Soil properties of the upper layer and the measurement and simulation periods of the investigated sites

site		pH*	clay	silt	sand	C_{org}	measur. period	simu. period
A:	pasture land [1]	–	25.0	70.0	5.0	3.0	87–88	87–88
B:	loamy soil	7.3	18.0	80.3	1.7	0.94	86–88	86–88
C:	clayey soil	7.7	27.5	69.5	3.0	1.40	86–88	86–88
D:	sandy soil	6.3	4.3	16.0	79.7	1.22	86–88	87–88
E:	peaty soil	6.3	4.0	9.2	86.8	7.78	86–88	87–88
F:	sandy soil	5.5	3.4	11.4	85.2	0.87	86–88	87–88

* (0.02 N $CaCl_2$) [1] (soil properties estimated)

In order to register the poulation dynamics soils samples were taken from all sites at two or four week intervals. One of the investigated sites is pasture land which was chosen for simulating the population dynamics in the absence of arable farming. This site was investigated only during the years 1987–1988. The climate data were measured at site B and site D. For the simulation the mean daily soil temperature at the depth of 5 cm was taken. Because different crops are grown on the other sites and the thermal conductivity as well as the heat capacity of the soil varies with the soil texture and the water content, slight differences in the temperature regime between the sites can be expected.

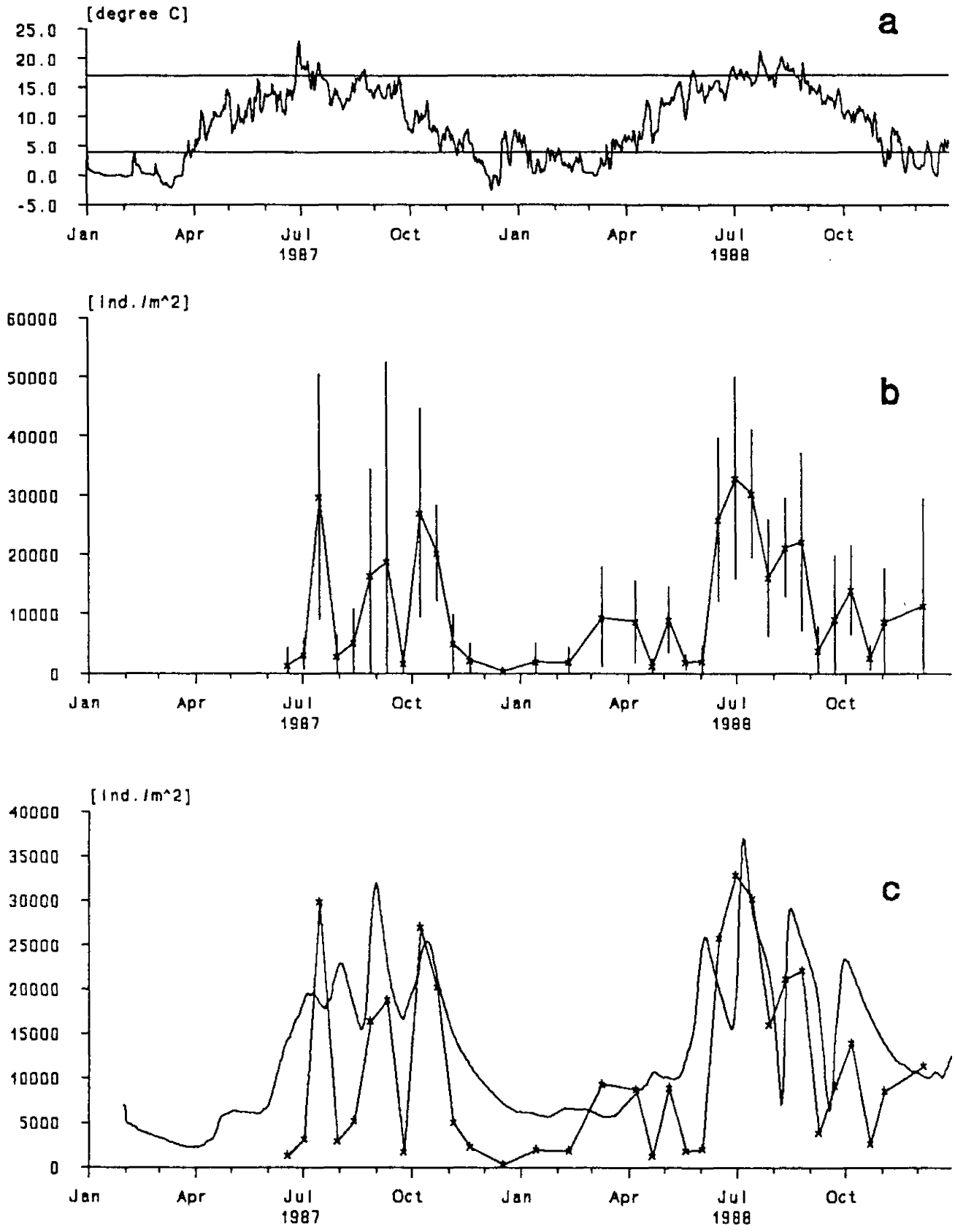

Fig. 6. Comparison between measured (*) and simulated population size on site A (pasture land). 6a) time course of soil temperature at the depth of 5 cm. The two vertical lines indicate the lower (4 °C) and upper (17 °C) temperatures used in the study of Sharma & Kevan (1963). 6b) Measurements and standard deviation. 6c) Simulated and measured time course

The samples were taken using a core-sampler up to a depth of 15 cm. The soil core was divided into three equal parts to study the vertical distribution. Ten replicates were taken from each site. The extraction of the mesofauna was done using a modified MacFadyen-extractor (MacFadyen 1961). To give an idea of the heterogeneity the mean values of the number of individuals caught and their standard deviation for site A (pasture land) is shown in Fig. 6b. It should be noted that the conversion factor between size of the core-sampler and m^2 is about 800 (e.g. 40000 Ind./m^2 = so individuals caught).
A first analysis of the dominance spectra and the population dynamics of other Collembola observed on the sites is given by Röske (1900, 1993).

Results

The model already described was applied to simulate the population dynamics on all six sites. Because climate data from the northern catchment are available only for the years 1987 – 1988 the simulation period of these sites is limited to this period (cf. Tab. 4). Due to the measurement technique only juvenile and adult Collembola are registered. Therefore, the field measurements are compared with the sum of the simulated juveniles and adults.
It is obvious that good simulation results can be achieved by calibrating the model at each site separately by varying every parameter, but in this case the model cannot be evaluated. To validate the model approach it is necessary to apply the calibrated model to a site not used in the calibration procedure. Therefore, it is necessary to distinguish between parameters describing the Collembola and site dependent parameters, e.g. initial condition and site capacity. In this model application the parameters pertaining to the development of the Collembola were constant for all sites.
After testing the model under constant climate it was calibrated on the pasture land (site A). The pasture land was chosen because this site is not cultivated, has an optimal moisture and temperature regime, and offers a constant source of food for the animals. The temperature measured on site B are shown in Fig. 6a. Two horizontal lines indicate the range between 4° and the 17 °C which are the minimum and maximum temperatures used in the laboratory studies of Sharma & Kevan (1963). Fig. 6b shows the measurements (mean value of the ten replicates) and their standard deviation. The simulation results using this temperature regime can be seen in Fig. 6c. Considering the large variability within the ten replicates the simulated and observed time courses compare well.

Table 2. Collembola-specific model parameters

survival probability eggs		0.983
survival probability juveniles		0.983
survival probability adults		0.983
development rate eggs	q	2.2
	T_{opt}	20.0
	T_{max}	28.0
	r_{max}	0.18
development rate juveniles	q	2.0
	T_{opt}	22.0
	T_{max}	28.0
	r_{max}	0.08
development rate adults	q	2.3
	T_{opt}	18.0
	T_{max}	28.0
	r_{max}	0.06
fertility	q	3.9
	T_{opt}	17.0
	T_{max}	20.0
	r_{max}	0.37
	offset	0.125
exponent of the $\varphi(k)$ function (v)		6.0
exponent of the Weibull-distribution (β)		10.0

To gain these results it was necessary to adjust the site capacity k_{max} to the value of 20000 ind./m^2. The survival probability was increased (0.983 for all stages compared to 0.980 observed for eggs by Sharma & Kevan, 1963). All other parameters were taken from the paper of Sharma & Kevan (1963). The parameter values are given in Tab. 2.
For validation the calibrated model was applied to simulate the time course of five additional sites. Two groups of parameters were distinguished: Collembola specific and site specific parameters. In order to create a model which is transferable to other situations it is necessary to take the Collembola-specific parameters from the simulation of the pasture

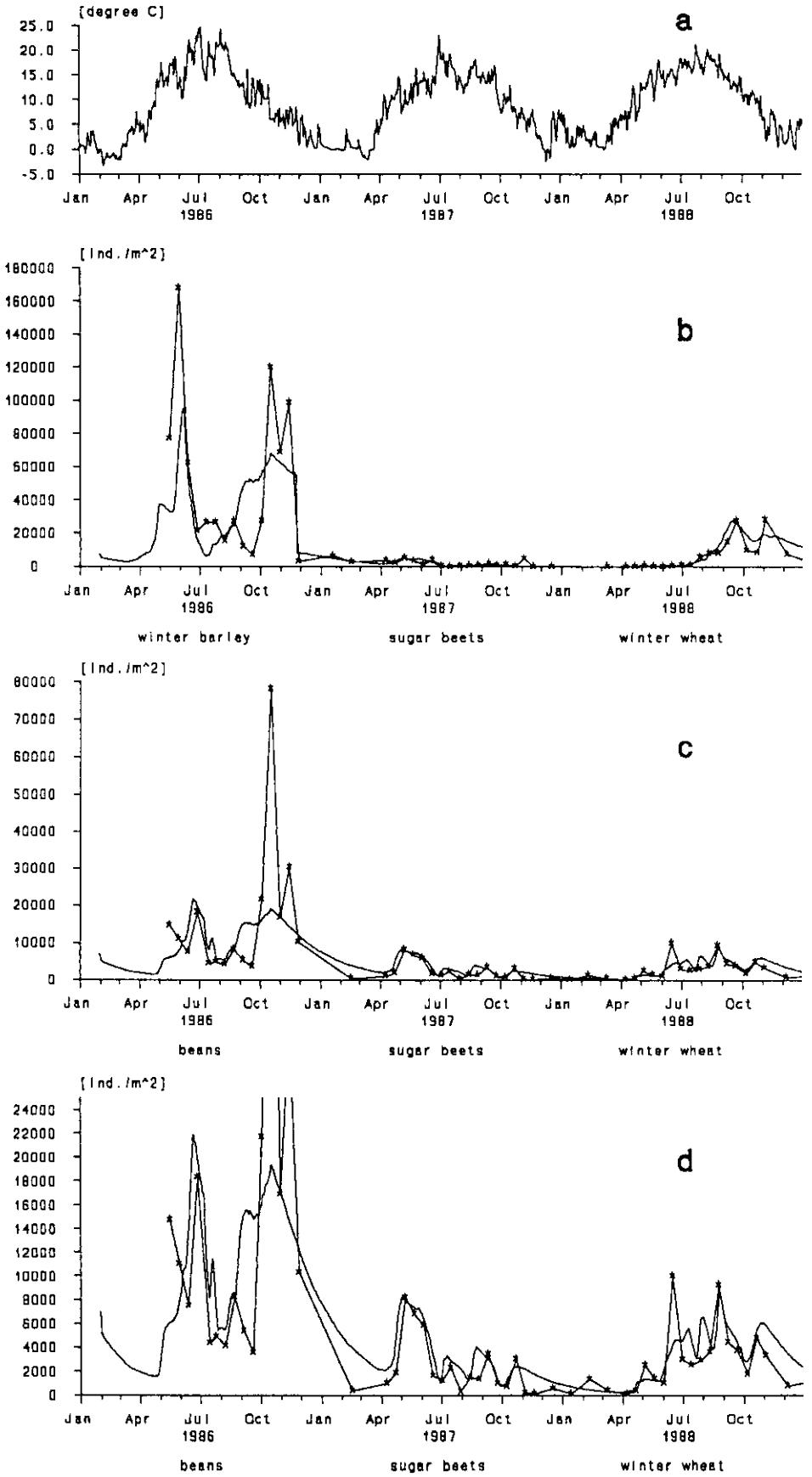

Fig. 7. Comparison between measured (*) and simulated population size on site B (Fig. 7b, loamy soil) and site C (Fig. 7c and 7d, clayey soil, different scales). 7a) time course of soil temperature at the depth of 5 cm

land without any modification. The simulation of the other sites is further complicated by tillage, temporal variable plant cover, larger amplitudes of the soil temperatures and of the soil water regime.

First the model was applied without considering any further environmental impacts. The deviation between simulation and measurements was analyzed in order to identify the times on which the divergence starts. Two major effects have to be distinguished: a) slow decrease of the population size during a long period of time (several weeks) and b) rapid decrease of the population size. In the first case the additional decrease of the population size which cannot be explaned by the mean survival probabilities can be related to a period of extreme dryness. This can be considered in the model by a decreased survival probability during the period of dryness. In the second case the decrease in population size can be explained by cultivation. This is handled in the model by partly destroying the population. Sensitivity analyses showed that considering water stress and tillage operations will change the population size but not the temporal pattern.

Starting with the parameter set from the pasture land the site specific parameters of the five sites were calibrated (cf. Tab. 3 and 4). Fig. 7 shows the comparison between measurements and simulations on the sites B (loam) and C (clay). On these sites a period of extreme dryness had to be considered in 1986. Unfortunately at that time no measurements of the water regime were carried out. But this was the only simulation year when large cracks could be observed in the soil on the clay and loam site. In this period the survival probability was reduced. Furthermore on the loam site a tillage operation caused a decrease in population size of about 85%. During 1987 only a small population could survive under sugar beets. Due to this the increase in population size is rather late (September 1988) compared to the clay site where the increase starts in June 1988. Both time courses were simulated well using the parameters given in Tab. 2 and 3. Because no tillage operations and no water stress had to be considered in 1987 and 1988 this good result is obtained by the model and not by calibrating the environmental impacts.

In contrast to the southern catchment the northern is irrigated. Therefore the water regime is balanced until harvest. After harvest the sandy soil dries out very quickly and water stress may occur. Due to the pore size distribution and the water retention curves of the upper layer this can be assumed to occur frequently.

Table 3. Site-specific model parameters (southern catchment)

A: *pasture land*		
simulation period		31. 01. 87 – 31. 12. 88
site capacity		20000 ind./m^2
water stress		–
tillage		–
B: *loamy soil*		
simulation period		31. 01. 86 – 31. 12. 88
site capacity	31. 01. 86 – 15. 05. 87	150000 ind./m^2
	16. 05. 87 – 31. 12. 87	550 ind./m^2
	01. 01. 88 – 31. 12. 88	25000 ind./m^2
water stress	08. 06. 86 – 10. 07. 86	$P_s = 0.87$
tillage	25. 11. 86	85% destroyed
C: *clayey soil*		
simulation period		31. 01. 86 – 31. 12. 88
site capacity	31. 01. 86 – 15. 05. 87	20000 ind./m^2
	16. 05. 87 – 31. 12. 87	2500 ind./m^2
	01. 01. 88 – 31. 12. 88	5000 ind./m^2
water stress	08. 07. 86 – 28. 07. 86	$P_s = 0.87$
tillage		–

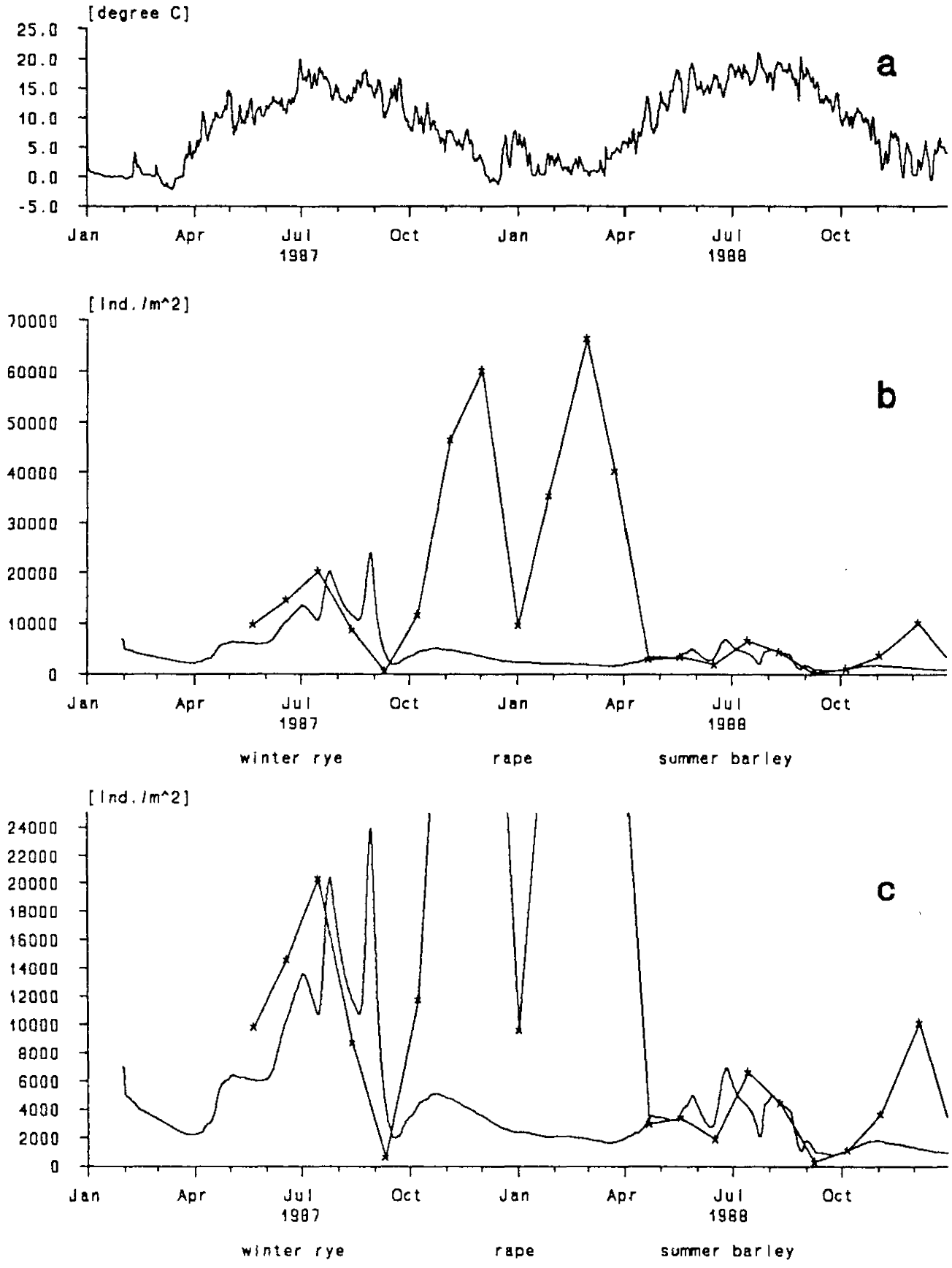

Fig. 8. Comparison between measured (*) and simulated population size on site D (Fig. 8b and 8c, sandy soil, different scales). 8a) time course of soil temperature at the depth of 5 cm

The simulation results of the three sites from the northern catchment can be found in Fig. 8 and 9. In every simulated year either tillage or water stress has to be considered (cf. Tab. 4). Because tillage operations, plants and applied pesticides are comparable to that from the southern catchment it may be concluded that the environmental conditions have a greater impact on the population size on sandy soils than on loamy or clayey soils.

From the investigations carried out by Vannier (1970) the critical soil suction for Isotomidae is known to be about 15000 hPa. At that critical soil suction the relative humidity of the soil air decreases and the mortality increases. Because of the large variability in water retention curves it is not possible to determine this critical threshold simply by measuring the water content. By applying a simulation model to forecast the soil water regime it is

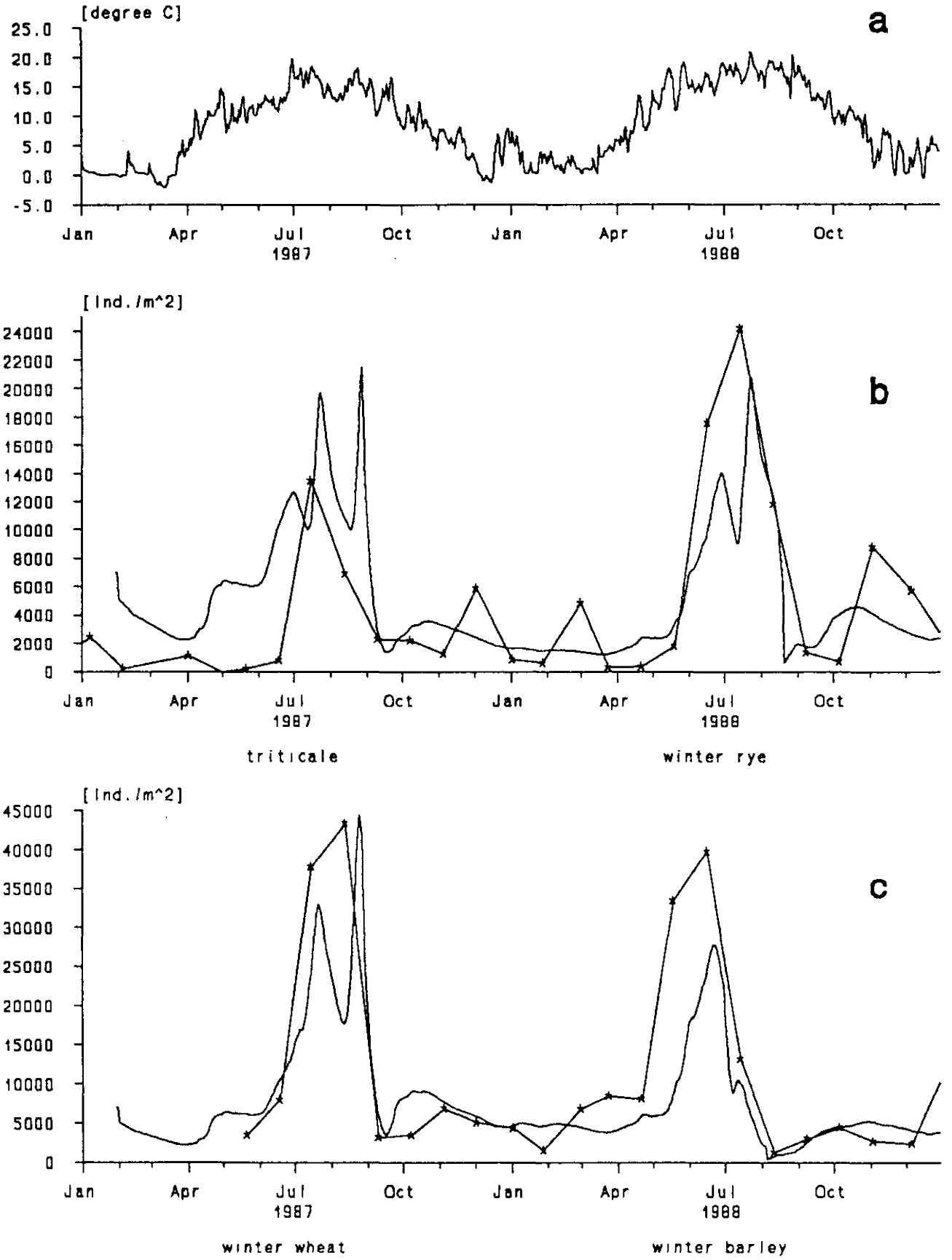

Fig. 9. Comparison between measured (*) and simulated population size on site E (Fig. 9b, peaty soil) and F (Fig. 9c, sandy soil). 9a) time course of soil temperature at the depth of 5 cm

possible to consider water stress in the population model automatically. In this case the decrease of the soil air humidity with increase of soil suction can be calculated by an Arrhenius type function. The effect of the water stress can then be considered by multiplying the survival probability by a correction factor depending on the soil air humidity.

The model failed in only one situation. On site D rape was planted during the winter of 1987–1988. The model was not able to simulate the population size observed at that time (cf. Fig. 8). Because not enough eggs were laid in summer 1987 the large population size in November could not be reached. Furthermore the second peak in February 1988 could not be simulated due to low temperatures and delayed development. As described earlier the calibrated fertility rate was only about 25% of that observed from Sharma & Kevan

Table 4. Site-specific model parameters (northern catchment)

D: *sandy soil*		
simulation period		31. 01. 87 – 31. 12. 88
site capacity	31. 01. 87 – 11. 04. 88	13000 ind./m^2
	12. 04. 88 – 31. 12. 88	4000 ind./m^2
water stress	31. 08. 87 – 17. 09. 87	$P_s = 0.87$
	20. 08. 88 – 10. 09. 88	$P_s = 0.87$
tillage		–
E: *peaty soil*		
simulation period		31. 01. 87 – 31. 12. 88
site capacity		12000 ind./m^2
water stress	28. 08. 87 – 17. 09. 87	$P_s = 0.87$
tillage	20. 08. 88	90% destroyed
F: *sandy soil*		
simulation period		31. 01. 87 – 31. 12. 88
site capacity		25000 ind./m^2
water stress	28. 08. 87 – 17. 09. 87	$P_s = 0.87$
	01. 07. 88 – 30. 07. 88	$P_s = 0.87$
tillage	05. 08. 1988	80% destroyed

which leads to good results on the other sites. It may be possible that under optimal conditions this mean fertility rate can increase significantly due to parthenogenesis. This hypothesis can only be proved by further investigations.
In contrast to the southern catchment the measurement interval in the northern catchment in the years 1987 – 1988 was four weeks. A linear interpolation between measurements as given in Fig. 8 and 9 leads to the impression that the simulation is totally different from the observation. But looking at short intervals (e.g. July – October 1987) on site D the measurements show a decrease in population size which is confirmed by the simulation. The simulation shows two additional peaks between the measurements which are in agreement with the observations from the southern catchments where the measurement interval was two weeks.

Discussion and Conclusion

This model is able to simulate the population dynamics of *I. notabilis* under natural conditions. Comparisons with measurements of six different sites from two catchments show a good aggreement. On two of the six sites the simulation period was three years including two winter periods. Due to the non-linear description of the temperature dependent development rate it was possible to simulate summer and winter periods without changing any model parameter.
After calibrating the model on one site it was validated on five other sites with different soils and plant covers. The model structure could be validated because it was not necessary to change parameters pertaining to the population dynamics while transferring the model to other conditions. Only parameters like site capacity or tillage effectes were calibrated on each site but these parameters influence only the population size and not the population dynamics.
The temporal variability between different years on one site can be quite high e.g. on the loam site the simulated population size in 1986 was about 95000, 1987 about 500 and 1988 about 20000 ind./m^2. From these data a critical minimal population size, which is sometimes discussed while estimating the impact of pesticides on Collembola cannot be determined.

The plants seems to have the main impact on the population size. Under cereals the population size is about 20000 ind./m^2 whereas under sugar beets 500 to 3000 ind./m^2 can be observed. Further investigations are necessary to quantify the effects of crops and soils on the maximum population size.
It should be noted that during the simulations carried out the application of pesticides caused no impact on the population dynamics of *I. notabilis*. Furthermore only a few of the tillage operations influence the population size. Because the population was partly destroyed only three times no general rules for considering tillage operations could be gathered from these simulations. While analyzing the population dynamics without a simulation model wrong conclusions may be drawn from correlating the decrease in population size with tillage or pesticide application. Therefore the environmental impact can only be evaluated by comparing the observed temporal pattern with results from a simulation model.
This results are remarkable insofar as this is the first attempt to simulate the population dynamics of Collembola under field conditions. It is obvious that not all questions can be answered in a single study although a closed concept for analyzing field data using laboratory experiments and a simulation model is presented. Nevertheless, from this study the following conclusions can be drawn:

- The population dynamics of *I. notabilis* is well described by the extended Leslie model.
- In contrast to regression models this model approach has predictive power because it calculates the population dynamics for different stages based on biological knowledge.
- Due to the structure, the model is applicable not only for *I. notabilis* but for organisms which develop in different stages like mildew, nematodes and Diptera.
- The parameters pertaining to the population dynamics can be transferred from laboratory experiments to field conditions.
- The parameters pertaining to the maximum population size were calibrated in this study, – they show a correlation with the crops grown on the investigated sites.
- An influence of the soil type on the population dynamics could not be ascertained due to the determinative effect of the crops.
- Only a few management operations influence the population dynamics of *I. notabilis*.

It is obvious that due to different population dynamics the dominance spectra also vary in time. Therefore, for a complete analysis of the mesofauna, the population dynamics of each species has to be analyzed. Unfortunately, only a few international papers deal with the temperature dependent development of soil animals. These investigation are indispensable for applying a simulation model to forecast the population dynamics.
Comparing the measurement intervals of the northern and the southern catchment it can be concluded that for *I. notabilis* a four week interval is too large. In order to monitor the population dynamics of different Collembola species it is necessary to adjust the measurement interval according to the life history (egg to egg) of the different species.

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